



Brook lamprey survival in the dry riverbed of an intermittent stream

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ARTICLE INFO

Keywords:

Hyporheic refuge hypothesis
Temporary river
Refuge
Drought
Lamprey
Climate change

ABSTRACT

Intermittent streams account for approximately one half of the global river network, and are especially common in arid and semi-arid regions. These systems are inhabited by several fish species that are adapted to their natural flow intermittency. While many fish species rely on permanent pools or perennial reaches to survive during the dry season, our knowledge regarding fish survival strategies in dry reaches is incomplete. Our observations revealed that ammocoetes (i.e. lamprey larvae) of a non-parasitic brook lamprey (*Lampetra* sp.) survived in the hyporheic zone of an intermittent stream in the absence of surface water for at least 22 days. This is the first reported observation of ammocoetes persisting in the hyporheic water after loss of surface water, a behavior that has been previously reported for just a few fish species.

1. Short communication

Intermittent streams cease to flow at some point in space and time, and are present in all climate areas, accounting for approximately one half of the river network globally (Datry et al., 2014) and more in arid and semi-arid regions. For instance, non-perennial streams account for 66% of the river network in California and > 90% in Arizona (Levick et al., 2008). However, most research on rivers has overlooked intermittent streams and, thus, current paradigms in river science and management have emerged from studies of perennial streams. Despite growing awareness about the importance of intermittent streams for supporting rare (e.g. Bogan, 2017) and imperiled species (e.g. Rodríguez-Lozano et al., 2015; Hwan et al., 2018), there is limited knowledge regarding strategies that allow aquatic species to inhabit those systems. Previous research has focused mainly on the recolonization ability of aquatic organisms and the importance of isolated pools as a refuge during dry periods, while the survival of aquatic animals in the absence of surface water has received less attention. Palmer et al. (1992) introduced the ‘hyporheic refuge hypothesis’, highlighting the vertical movement of benthic organisms into the hyporheic zone (i.e. the water-saturated interstitial spaces in the streambed) as a refuge during disturbance events and, ultimately, a source of colonists following the event. This hypothesis was initially proposed to describe the adaptation of meiofauna to flood events, but recent research has revealed that several aquatic macroinvertebrate species can take refuge in the subsurface water present in the hyporheic zone during dry periods in intermittent streams (Stubbington, 2012). Many fish species inhabit

intermittent rivers and, in general, they rely on isolated pools or perennial reaches as refuges during dry periods. Although that is the general pattern, here we ask: can fish take advantage of the subsurface water in the hyporheic zone as a refuge in intermittent streams when surface water is absent?

With the goal of monitoring the fish populations of the Coyote Creek headwaters, located within Henry W. Coe State Park, central California, USA, we sampled ten stream pools on a monthly basis through the summer of 2017. Coyote Creek is a Mediterranean climate, intermittent stream which becomes reduced to a series of isolated pools and dry reaches throughout the summer dry season. During the course of our research, one of the ten monitored pools dried on September 27th (37°06′45″N; 121°28′40″W), after which it lacked surface water until the onset of the fall rains. Seven days before the pool lost its surface water completely, the isolated pool was characterized by a total length of 3.2 m, a maximum depth of 12 cm, and a total water volume < 0.25 m³. At this pool, we captured 23 ammocoetes (i.e. lamprey larvae) of a non-parasitic brook lamprey (*Lampetra* sp.; 39–146 mm total length) and 60 Coastal roach (*Hesperoleucus venustus*; < 40 mm fork length). The lamprey fauna of California is highly diverse, and the non-parasitic brook lamprey found in Coyote Creek is of uncertain taxonomic status (Reid et al., 2011; Boguski et al., 2012).

To explore whether live fish were present in the interstitial waters within the hyporheic zone following loss of surface water, we sampled the hyporheic zone below the dry riverbed of the focal stream pool on two occasions: 11 and 22 days after the pool completely dried. We excavated a pit (about 40 cm in diameter, 15 cm in depth) at the lowest

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Fig. 1. The Coyote Creek streambed (upper, photo by P. Rodríguez-Lozano); a *Lampetra* sp. ammocoete from Coyote Creek (middle, photo by P. Rodríguez-Lozano; bottom, photo by S. M. Carlson).

point/elevation of the pool until we encountered the water table (4 cm depth, 11 days after the pool dried, and 8 cm depth after 22 days). We then used an electrofisher to sample the exposed hyporheic water (voltage used ranged 100–120 V; initial short pulses were used to induce ammocoetes to emerge). While we did not find any Coastal roach, we retrieved, in total, eight live ammocoetes of the non-parasitic brook lamprey (5 ammocoetes were retrieved on the first sampling occasion and 3 individuals on the second sampling date). The size of these eight individuals (44–132 mm total length; 0.16–4.24 g) was within the size range of ammocoetes sampled from seven pools with surface water in Coyote Creek ($N = 71$; 30–146 mm total length; 0.14–5.18 g). Our observations revealed that *Lampetra* sp. ammocoetes survived in the water of the hyporheic zone of an intermittent stream in the absence of surface water for at least 22 days (see Fig. 1).

To the best of our knowledge, this is the first reported observation of lamprey ammocoetes persisting in the hyporheic water after loss of surface water. Although it is well known that ammocoetes inhabit the shallow hyporheic zone where they create burrows and feed by filtering the water column until they metamorphose into the adult stage, this is the first report of ammocoetes persisting in the interstitial subsurface

water after the loss of surface water. Other studies have reported fish species using the hyporheic zone while there is surface water (e.g. Jurajda and Rulík, 2001), however use of the hyporheic zone during absence of surface water has been rarely reported for other fish species (but see Stegman and Minckley, 1959; Kawanishi et al., 2013). Similar to our findings, Kawanishi et al. (2013) described that the spinous loach (*Cobitis shikokuensis*, Cobitidae, Cypriniformes), a small benthic fish that inhabits the streams of the Shikoku Island, Japan, survived in the hyporheic zone at least 20 days after complete loss of surface water and subsequently recolonized the stream surface upon rewetting. Our focal pool was dry for 50 days at the end of the summer (flow resumption occurred on November 16th 2017), and we do not know if ammocoetes were able to survive for the entire dry period at that particular site. However, due to the high spatial variability of the system, other stream reaches dried for shorter periods – some dried for < 22 days, while some pools persisted for the entire dry period. Our observations confirm that persistent, permanent pools and the hyporheic zone associated with dry stream reaches can both function as refuges for brook lamprey during the dry season.

Lampreys are an ancient lineage of jawless fish species (order Petromyzontiformes) that have been understudied, particularly in intermittent streams. Consequently, their distribution, conservation status, and phylogeny remain unclear (Quiñones and Moyle, 2015). In California, several lamprey species are currently listed as Species of Special Concern by the California Department of Fish and Wildlife (Moyle et al., 2015). Four lamprey species from the west coast of North America (*Entosphenus tridentatus*, *Lampetra richardsoni*, *L. ayresii*, and *L. hubbsi*) have been nominated for listing as threatened or endangered under the US Endangered Species Act of 1973, but the petition was deferred due to lack of information on species' distributions, population structure, and ecology (USFWS, 2004). Consequently, there has been an increase in research on lampreys, with a focus on delineating species' distributions in the US Pacific Northwest (Reid and Goodman, 2016). Our observations have implications for current efforts to determine the distribution and status of brook lamprey populations. In particular, our results emphasize the need to also sample the hyporheic zone of dry riverbeds in lamprey monitoring programs, for which it is necessary to develop new sampling protocols.

Other fish species present different adaptations to survive in the absence of surface water. The best-known example is the African lungfish (*Protopterus* spp.), which can burrow in the stream sediment, secrete a protective mucus from the skin to form a hardened cocoon, and aestivate (Smith, 1931). In doing so, this fish can survive the total absence of interstitial water for multiple years. Other fish species in Africa, Asia, Oceania, Central America, and South America can aestivate without forming cocoons (Ogston et al., 2016), e.g. South American lungfish (*Lepidosiren paradoxa*), the African catfish (*Clarias gariepinus*), and the Australian salamanderfish (*Lepidogalaxias salamandroides*). Killifish adapted to the temporary waters of Africa (Nothobranchiidae) and South America (Rivulidae) have an annual life-cycle which growth and reproduction are condensed into a short season, while their eggs are capable of surviving in the absence of water (Furness, 2016; Vrtilek et al., 2018). Both adaptations - aestivation and dormant eggs - are rare among fish species and undescribed for fish species inhabiting North America and Europe, and differ from the behavior observed for *Lampetra* sp... As far as we know, *Lampetra* sp. is not able to aestivate and is not adapted to the absence of water, but is able to survive in the interstitial subsurface water during dry periods of surface water absence. Both *Lampetra* sp. and *C. shikokuensis*, as well as fish species that aestivate are characterized by elongate and flexible bodies, suggesting that morphology could be a critical factor controlling access to the stream subsurface.

With climate change and water abstraction, some perennial streams are shifting to intermittent hydrological regimes, and drought severity and the duration of the dry phase of intermittent streams are projected to increase (Carlisle et al., 2011). Therefore, it is important to

understand if the hyporheic zone will serve as a refuge for brook lamprey species and other fish species in intermittent streams. Among the questions that need to be addressed in the future are: (1) Which other fish species can survive in the hyporheic zone in the absence of surface water? (2) Which factors control the refuge potential of the subsurface interstices for fish species, including physical habitat parameters (e.g. sediment porosity) and fish morphological, behavioral, and physiological traits? (3) For how long can fish survive within the hyporheic zone in the absence of surface water? (4) How do climate change and other human stressors (e.g. channel modifications, water abstraction) threaten the refuge function of the hyporheic zone? Research on these topics will help to increase our understanding of the role of the hyporheic zone as a refuge for fish in intermittent streams and will improve our knowledge on the distribution and status of freshwater fish species. Additionally, such research would increase our understanding of the vulnerability of fish species to anthropogenic impacts, which can guide conservation and management efforts. The expansion of the 'hyporheic refuge hypothesis' to fish species will lead to new research that will improve our understanding of fish ecology in intermittent streams.

Acknowledgements

Coyote Creek is the ancestral homeland of the Amah Mutsun Tribal Band. Thanks to Hana Moidu and Brian Kastl for their assistance in the field and to the staff of Henry Coe State Park for processing our research permit and arranging access. We are grateful to the two anonymous reviewers who helped us to improve this article. Our work was approved by the UC Berkeley Animal Care and Use Committee (Permit #AUP-2016-12-9393); California CDFW Scientific Collecting Permit is SC-001572. P. Rodríguez-Lozano was supported by a Ramón Areces Foundation Postdoctoral Scholarship.

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